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Commentary

Constraints on evolutionary shifts in cooperative breeding

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Bergmüller et al. (2007) provide an insightful review of four key issues surrounding the evolution and maintenance of cooperative breeding, and suggest how these can be integrated into a single hierarchical classification of mechanisms maintaining cooperative behaviour. I agree that this integrative approach may be useful in creating a unified framework that allows us to analyze different forms of cooperation in a consistent way. Cooperative breeding offers an ideal context in which to test more general theories of cooperation, provided that it is studied at the appropriate level, focusing on the responses of individuals to changes in the behaviour of others. The basic idea is that evolutionary interests drive subordinates to trade-off current helping investments against (future) returns. To support their search for future directions I offer three comments.

Firstly, their hierarchical classification model for cooperative behaviour is based on four key questions. The first two questions ask whether or not an individual invests in a partner and whether or not this initial investment elicits a return investment by the beneficiary. Return investment is considered here as a costly response. The evolution of investment should be driven by the relative costs and benefits of investment (e.g., Maynard Smith, 1977; Clutton-Brock, 1991). However, in general it is hard to determine whether individuals in cooperatively breeding species actually invest in a partner, and subordinates may often be wrongly categorized as non-helpers. As stated in Bergmüller et al.'s (2007) review, this is because in some societies, although subordinates might not show active help, they may nevertheless increase the fitness of the breeders through indirect effects like predator dilution (e.g., Clutton-Brock, 2002). Such a scenario could also explain why apparently non-cooperative individuals, that appear to offer no investment, are tolerated in some communally breeding species. However, according to the hierarchical classification of mechanisms that can maintain cooperative behaviour, the first question is to ask whether or not an individual invests in a partner. If not, then cooperative behaviour is explained by 'by-product mutualism'. Given that by-product mutualism results when individuals generate benefits for others as a side-effect of performing a selfish act (West-Eberhard, 1975; Brown, 1983), it is hard to envisage that a non-selfish act (such as group augmentation without investment) would be automatically categorized as by-product mutualism according to Fig. 1 in Bergmüller et al. (2007). In addition, a major problem is to show whether group augmentation involves investments or not. This is perhaps the most difficult concept in the cooperative breeding literature because one could potentially refer to every productivity or survival effect that increases with group size as 'group augmentation', when it might in fact be impossible to determine what is really going on. Alternatively, subordinates may be wrongly categorized as non-helpers because most studies have focused solely on subordinates provisioning offspring, ignoring other potential types of helping behaviour such as nest building and predator defence (Heinsohn, 2004). In some cooperatively breeding systems, individuals presumed to be non-helpers are not as uncooperative as they appear. For example, in the cooperatively breeding noisy miner *Manorina melanocephala*, a considerable fraction of subordinates that were never seen to provision the young did help intensively in mobbing predators. Furthermore, bad provisioners contributed more to mobbing than good provisioners (Arnold et al., 2005).

The above example brings me to my second point. Bergmüller et al.'s (2007) hierarchical classification model assumes there is plasticity in helping decisions and thus in the degree of investment by the helper. This is not entirely correct. Although many studies have focused on the role of life history and ecological factors, the proximate mechanisms underlying helping behaviours have received considerably less attention. Individual differences in the frequency and type of helping behaviour (division of labour) might not be fixed for life, but they could still be the result of age-dependent polyethisms. For example, in white-winged choughs *Corcorax melanorhamphos*, the amount of help increases sharply with age (Heinsohn and Cockburn, 1994). On the other hand, in blue jays *Cyanocitta cristate*, labo-

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ratory tests have shown that some individuals were consistently more cooperative for mutual food gain than others (Stephens et al., 2002). In great tits *Parus major*, some individuals are consistently more aggressive (e.g. towards competitors) than others (Drent et al., 2003). Social groups can thus be made up of individuals specializing in different helping behaviours and/or performing a number of helping behaviours to differing degrees. So far, division of labour among members of cooperatively breeding groups has mainly been studied in eusocial insects, where individuals often show morphological differentiation associated with specialization for particular tasks (e.g., Keller and Vargo, 1993; Traniello and Rosengaus, 1997). However, recent studies have demonstrated consistent differences in the behaviour shown towards the same stimuli between individuals from different populations (Taborsky, 1994; Gross, 1996) and within the same population (Dingemanse et al., 2002; Drent et al., 2003). Although the review by Bergmüller et al. (2007) focuses mainly on cooperatively breeding vertebrates, plasticity in helping behaviour may be limited in these systems too. Among cooperative birds and mammals, in which morphological differences between breeders and helpers are unusual (Solomon and French, 1997), consistencies in type or amount of helping behaviour can arise even in the absence of extreme specialisation (e.g., Lacey and Sherman, 1990; Heinsohn and Cockburn, 1994; MacColl and Hatchwell, 2003; Arnold et al., 2005). Such individual propensities for performing specific helping behaviours are suggestive of behavioural syndromes (or personality types; Sih et al., 2004) and are an important source of non-plasticity in behaviour which should be included in Bergmüller et al.'s (2007) decision tree. If there is individual consistency in the performance of a specific behaviour, individuals behave in a particular way regardless of the circumstances; some individual types may behave less optimally than others, which makes the hierarchical classification approach too simplistic. However, one should also bear in mind that if there is evidence for individual consistency in the performance of a specific behaviour, this does not necessarily imply a genetic basis to that behaviour. An alternative possibility is that the type and amount of helping behaviour is determined during some critical period of development (hormone levels through maternal effects; imprinting). On the other hand, apparent lack of consistency in behaviour does not preclude a strong genetic component for the parameters of the reaction norms for different individuals. All individuals may show variability in helping behaviour under different circumstances, but their propensity to help in a given state, or their threshold for help, may be determined mainly by the genes. It has been assumed that differences in the behaviours and strategies employed by individuals to maximize their inclusive fitness are largely due to behaviourally plastic responses to the environment (Sih et al., 2004; Pennisi, 2005). However, the behaviour that we see can also reflect genetic differences among individuals. Despite the fact that genetic variation lies at the heart of evolutionary adaptation, we are usually unaware of the genetic mechanisms underlying the strategies we model or study empirically (Grafen, 1991). To give an example, recent work on rodents of the genus *Microtus* (voles) shows that length polymorphisms in the regulatory regions of genes have important impacts on the expression of genes that affect social behaviour, leading to behavioural variation between individuals (Hammock and Young, 2005). In male prairie voles, long-allele individuals engaged in social interactions more readily than short-allele individuals. It is therefore plausible that genetic variation generates individual variation within a species in the propensity to cooperate. In other words, alternative tactics may be exhibited by different types of individuals (genotypes). Recent work in a range of species has revealed a strong genetic component to behaviour (Bakker, 1994; Koolhaas et al., 1999; Pervin and John, 1999; Insel and Young, 2000; Dingemanse et al., 2002; Fitzpatrick et al., 2005; Hammock and Young, 2005). Therefore, both the genetic and environmental determination of behaviour should be incorporated as proximate factors shaping the evolution of cooperative breeding.

My third comment concerns the measurement of reciprocity. According to Bergmüller et al.'s (2007) hierarchical classification of mechanisms that can maintain cooperative behaviour, when investment by both partners occurs, one has to ask whether it is the initial investment that directly elicits the return investment. The existence of reciprocity is hard to measure in natural environments in the first place because it may be almost impossible to provide evidence for contingent acts, i.e. to make a connection between a received benefit and the returned investment, except for very artificial settings which are hard to interpret (see Noë, 2006). Second, as cooperatively breeding vertebrate species are often relatively long-lived (Arnold and Owens, 1998; Hatchwell and Komdeur, 2000), the potential for mutual reciprocity exists. However, despite this potential, it may be that the majority of studies on such species have not progressed for long enough for reciprocity to be identified. In long-lived animals it has been suggested that the increasing mortality costs of reproduction with age may mean that older individuals are able to gain greater fitness benefits by helping their offspring to breed than by breeding themselves (Williams, 1957; Hamilton, 1966). The presence of older, reproductively experienced individuals that engage in kin-directed cooperative behaviour is common in humans (Lahdenpera et al., 2004) but has been documented in only a few other mammal species. For example, in lions, *Panthera leo*, older females nurse their daughters' cubs (Pusey and Packer, 1994); in baboons, *Papio anubis*, older females groom and intervene in disputes on behalf of descendent kin (Gouzoules and Gouzoules, 1987); and in humans, mothers help feed their daughters' and nieces' offspring (Hawkes et al., 1998). Although it seems plausible that other cooperatively breeding bird species may show this pattern too, especially those species with redirected helping where individuals that lose their own nests become helpers at the nests of kin, e.g. long-tailed tits, *Aegithalos caudatus* (Hatchwell et al., 2001), and western bluebirds, Sialia mexicana (Dickinson et al., 1996), no studies have reported such behaviour. On the one hand, delayed reciprocity in non-human animals might be a very rare phenomenon because of the cognitive requirements of book keeping. On the other hand, it may well be that this is not necessarily a rare phenomenon. Perhaps the majority of studies on long-lived, cooperatively breeding bird species, in which post-dominant, old-aged helpers would be expected to evolve, have not yet progressed for long

enough, nor been detailed enough, for such individuals to be identified. The possibility of post-dominant individuals engaging in kin-directed cooperative behaviour points to a new route to cooperative breeding.

The last point I want to make is that very few studies on resident species have provided adequate long-term data to quantify how current differences in reproductive allocation translate into changes in future inclusive fitness; delayed reciprocity can occur over a long time frame. While it should be clear that many phenomena found in social species cannot be fully captured by Bergmüller et al.'s (2007) hierarchical classification approach, their review represents an excellent attempt to integrate theoretical and empirical concepts for the evolution of cooperative breeding. A key challenge for both theoreticians and empiricists will be to integrate the multiple dimensions of allocation decisions and the conflicts that occur over such decisions.

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